

LOWER PERMIAN INSECTS FROM OKLAHOMA
PART 2. ORDERS EPHEMEROPTERA
AND PALAEODICTYOPTERA*

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Nature is always on the watch for our follies and trips us up when we strut.—R. W. Emerson

The discovery and exploration of the insect-bearing deposit in the Midco member of the Wellington Formation were made by Dr. Gilbert Raasch and me about forty years ago, just before the beginning of the Second World War. Preparation and publication of my first paper on the insects were necessarily deferred until after the war (Carpenter, 1947). By that time I had become convinced of the necessity of my studying in detail as many as possible of the Palaeozoic insects already described from European and North American deposits before continuing with the new material. Having spent several months before the war with the Commeny specimens in the Laboratoire de Palaeontologie in Paris and at least as much time on type specimens in museums in the United States, I had come to realize that many of the published figures and descriptions were unreliable and that most of the fossils had never been properly prepared for study, the body structures usually remaining hidden within the rock matrix. In part because of administrative duties at Harvard University after the war and in part because of the political conditions in Europe during the 1950's, I found it impossible to resume the study of such collections, especially in Paris and Moscow, until 1961. Since then I have been able to study the greater part of the more important collections and to publish on some of them, as time and occasion have permitted.

It now seems feasible for me to continue with the series of articles on the insects in the Midco beds. The collection at the Museum of

*Partial financial support of this research is gratefully acknowledged to the National Science Foundation, Grant no. DEB-09947, F. M. Carpenter, Principal Investigator. I am also indebted to the authorities of the Peabody Museum, Yale University, for the loan of type specimens.

Manuscript received by the editor October 15, 1979

Comparative Zoology contains about 8,000 specimens from that deposit. Most of them were obtained on the 1940 expedition but others were found from 1948 to 1957. All were collected at the localities listed in Part 1 of this series of papers (Carpenter, 1947).

Several years after the publication of that part, Dr. Paul Tasch of the Department of Geology, University of Wichita, Kansas, made several collections of fossils in extensions of the Midco beds or in associated deposits, mainly for the purpose of obtaining *Conchostraca*, in which he was especially interested; and with an associate, Dr. J. R. Zimmerman, he published a brief account of some of the insects found there (Tasch & Zimmerman, 1962). I am indebted to Dr. Tasch for placing at my disposal certain of the types in his collection, as well as some unstudied specimens.

The previous part of this series of papers dealt with the palaeopterous orders Megasecoptera, Diaphanopteroidea [included as a suborder of Megasecoptera], Protodonata, and Odonata. The present paper covers the remainder of the palaeopterous orders, the Ephemeroptera and Palaeodictyoptera.

Order Ephemeroptera

Three families of mayflies are known from Permian deposits: *Prottereismatidae*, *Misthodotidae* (including *Eudoteridae*) and *Palingeniopsidae*.¹

The first two of these families are well represented in the Midco beds. Adult mayflies, however, are not nearly as abundant in the Midco deposit as at Elmo, in Kansas. Over a hundred adults have been found in the Elmo beds in collections including about 8,000 specimens; only 26 adults have been found in the Midco beds in an approximately comparable collection. On the other hand, nymphs of mayflies, which are virtually absent at Elmo, are exceedingly abundant in the Midco beds.

Family *Prottereismatidae* Sellards

Prottereismephemeridae Sellards, 1907:345.

Prottereismatidae Handlirsch, 1919:63

Prottereismatidae Tillyard, 1932:237; Carpenter, 1933:489

Kukalovidae Demoulin, 1970:6 (new synonymy)

¹I consider this to be a distinct family, not synonymous with *Mesephemeridae*.

ADULTS

As now known the protereismatid adults ranged from moderate to large in size. The wings were elongate-oval, without maculations, the hind wings were similar to the fore pair in form and venation, and were only slightly shorter; the costal margin was serrate and prominent setae were present on at least some of the veins; the costal brace was very well developed in both pairs of wings; MA, almost immediately after its origin, coalesced for a short distance with the basal part of RS; RS had three complete triads, and both MP and CUA had a single triad; cross veins were very numerous. The antennae, although short, were relatively longer than in existing mayflies;

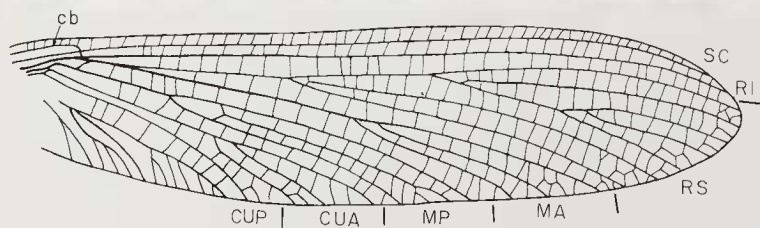


Figure 1 (above). *Protereisma directum*, n.sp. Photograph of holotype (fore wing), MCZ 5180a, Permian of Oklahoma. Length of wing, 26 mm.

Figure 2 (below). *Protereisma directum*, n.sp. Drawing of fore wing (holotype). SC, subcosta; R1, radius; RS, radial sector; MA, anterior media; MP, posterior media; CUA, anterior cubitus; CUP, posterior cubitus; cb, costal brace. The convexities and concavities of the veins are shown in figure 1.

sclerotized, dentate mandibles were present; the compound eyes were large; all legs were very long and slender, with five tarsal segments; the cerci and the median caudal filament were elongate, and the males possessed prominent claspers.

This family, known only from the Permian, was originally described from the Elmo beds. It is represented in the Midco collection by 18 specimens of adults, as well as by numerous nymphs. All of the Midco specimens belong to the genus *Prottereisma* and most of them to the large and striking species described below.

Genus *Prottereisma* Sellards

Prottereisma Sellards, 1907:347 [For generic synonymy see Tillyard, 1932, and Carpenter, 1933]

This genus, the only one at present in the family, is known by five species from Elmo. The insect described by Guthörl (1965) as *Prottereisma rossenrayensis*, from an Upper Permian deposit near Rheinberg, West Germany, is almost certainly a prottereismatid, but the published description is not sufficient for generic determination. Two other species, generally referred to as *Prottereisma uralicum* Zalesky (1946) (upper part of Lower Permian) and *P. apicale* (Martynov, 1927) (Upper Permian), both from the Soviet Union, are based on wing fragments that lack parts necessary for family determination. At the present time, therefore, the genus *Prottereisma* is definitely known only from the Lower Permian of Kansas and Oklahoma.

Prottereisma directum, n.sp.

Figures 1-4

Fore wing: length 26 mm, width, 6 mm; relatively long and narrow, the front and hind margins nearly straight; the venation, typical of *Prottereisma*, is shown in figure 2. Holotype: no. 5180ab, collected at locality 15-L, Noble County, Oklahoma, by F. M. Carpenter. This is a complete fore wing, with excellent preservation.

The two following specimens are designated as paratypes: no. 5182ab, consisting of the four wings and parts of the body. The fore wing is 31 mm long and 7 mm wide; the hind wing, 28 mm long and 6 mm wide. The body is preserved in dorso-ventral view; the head is 2 mm long and 4 mm wide across the eyes; the prothorax is 1.2 mm long and 4 mm wide; the mesothorax is 3 mm long and 4 mm wide;

the metathorax, 2.5 mm long and 4 mm wide. The abdomen (incomplete) is 25 mm long and 2 mm wide. The other paratype, no. 5181, consists of two fore wings and one hind wing; the fore wings are 28 mm long and 6.5 mm wide; the hind wing, 26 mm long and 6 mm wide.

In addition, there are 11 other specimens apparently belonging to this species, all isolated wings.

The wings of this insect differed from those of other *Protereisma* by their large size, slender form, nearly straight anterior and posterior margins and the longer costal brace. The species was only slightly larger than *P. insigne* Tillyard, from Elmo, but the latter had a much broader wing, with a strongly curved posterior margin. *P. directum* presumably had a wing spread as great as 70 mm, which is larger than that of most existing mayflies but much smaller than the Jurassic *Ephemeropsis tristalis*, which had a wing spread of about 90 mm.

Specimen no. MCZ 5182 is of special interest because of the excellent preservation of some parts of the body. The thorax, although somewhat crushed, shows the individual tergites very clearly (figure 4). Previously described specimens of *Protereisma* from Elmo have shown that the metanotum, although smaller than the mesonotum, was very much larger than it is in existing mayflies; this is shown in the accompanying photograph of *directum*. The pronotum consisted of a broad plate 1.2 mm long and 4 mm wide, about the same width as the mesonotum.

The serrations along the costal margins of the fore and hind wings of *Protereisma* were described by Tillyard in 1932. They are clearly visible on the specimens from Midco, especially those of *directum*. Tillyard was apparently not aware that the serrations were equally well developed or even more strongly developed on the hind margins of the wings of *Protereisma*. They are especially well preserved in the neotype of *Protereisma latum* Sellards, from Elmo (specimen MCZ 3419), and I take this opportunity to include two photographs (figure 5) of that specimen here, one showing the serrations along the costal margin and the other, those along the hind margin. The former also shows the setal bases on some of the veins. The serrated margins and setae on the veins are unknown in existing Ephemeroptera, but they were well developed in the extinct Palaeozoic orders Palaeodictyoptera, Megasecoptera, Diaphanopteroidea, and Pro-

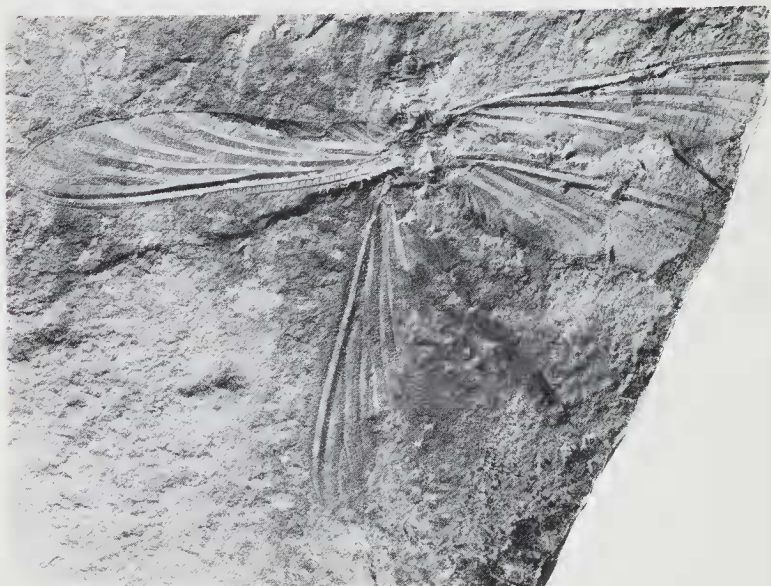


Figure 3. *Protoreisma directum*, n.sp. Photograph of paratype, MCZ 5182a, Permian of Oklahoma. Length of fore wing, 32 mm.

tononata. Serrated anterior margins are present in the existing Odonata and occur in isolated families of some other Recent orders, but their functional significance is not understood.²

In addition to the specimens of *directum*, there are several other isolated wings belonging to *Protoreisma*. One of these (MCZ 5185ab) appears to be a large specimen of *P. arcuatum* Sellards, described from Elmo. Six other specimens are clearly *Protoreisma* but are too incomplete for specific determination. Zimmerman (Tasch and Zimmerman, 1962) has figured a specimen of a mayfly from a deposit a few feet above the Midco insect bed in which the MCZ specimens were collected. I have not seen that specimen, which he identifies as *P. latum* Sellards. It might be that species, but if the costal brace is formed as shown in his figure, the insect could not even be assigned to the Protoreismatidae.

²In some existing insects the serrate margins appear to have a function in aggressive behavior. See Owen's account of the butterfly genus *Charaxes* (1961).

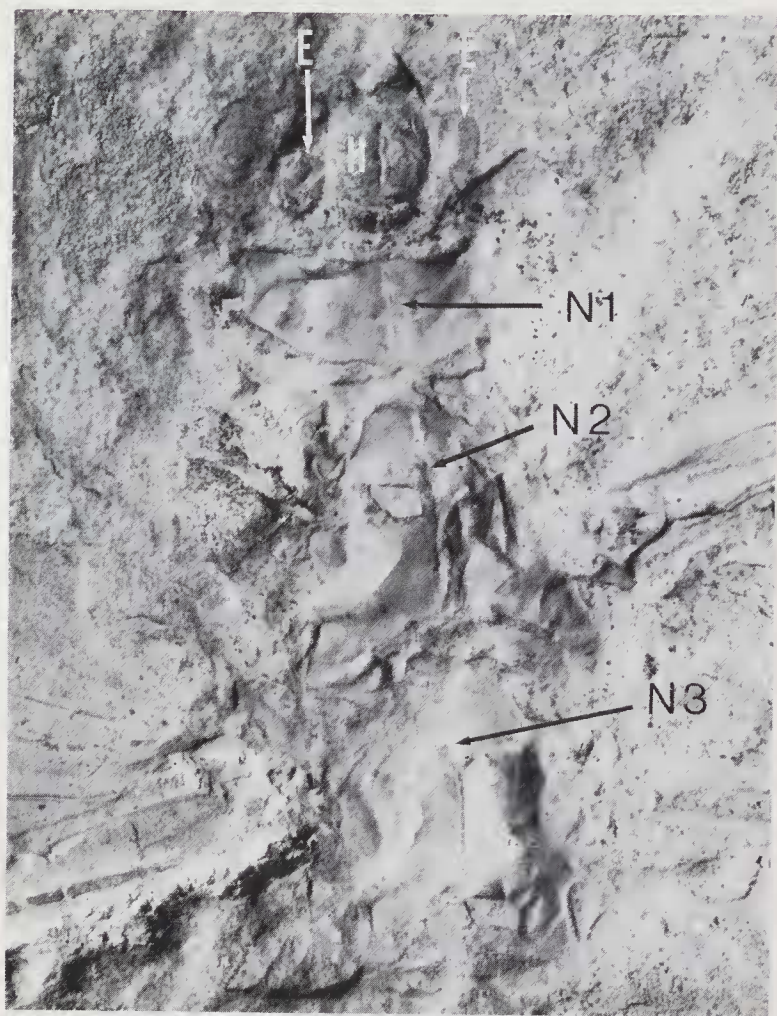


Figure 4. *Protoreisma directum*, n.sp. Photograph of head and thoracic region of paratype, MCZ 5182a, showing eyes (E), head proper (H), pronotum (N1), mesonotum (N2), and metanotum (N3). The left fore wing is preserved with its posterior margin directed anteriorly, as shown in figure 3. The dark circular object to the left of the head is a shell of a conchostracan.

Family Protereismatidae

NYMPHS

In 1968 Dr. Jarmila Kukalova, while making an extended visit to my laboratory at Harvard University, brought from Czechslovakia several fossil mayfly nymphs that she had collected in Permian beds in Moravia. Since only a very few, poorly preserved Palaeozoic mayfly nymphs were known at that time, I suggested that she might also study, along with her specimens from Moravia, some well-preserved specimens that I had collected in the Midco beds in 1940. However, since I had not yet published on or even studied carefully the mayfly adults in that deposit, I requested that the specimens be mentioned by numbers, instead of by new generic or specific names. The reason for that request, of course, was that the systematic position of the nymphs should be investigated in conjunction with similar studies of the adults in the same deposit. Accordingly, in Dr. Kukalova's published account (1969) of these nymphs, the fossils were identified as nymphs no. 1, no. 2, etc., of *Protereisma* sp., the generic assignment being probable but not certain.

However, my efforts to defer the naming of the Midco nymphs until the adult mayflies had been studied were defeated by Demoulin with his publication in 1969 of a paper entitled, "Remarques critiques sur des larves 'Ephemeromorpha' du Permien." In this publication Demoulin, without of course seeing any of the specimens, formally erected the new genus *Kukalova* and the new family *Kukalovidae* to receive the Midco species, which he named *americana* (type-species), and one of the Moravian species, *moravica*. The diagnoses were based on his interpretation of Kukalova's account. He also erected the new genus *Jarmila* for another of the Moravian nymphs, termed *elongata*, placing it in the new family *Jarmilidae*. The two new families were assigned to the extinct order *Archodonata*, and he established a new superorder, *Ephemeromorpha*, to include the *Ephemeroptera* and the *Archodonata*. Had Demoulin communicated his intentions to Dr. Kukalova or to me, we could have corrected his misconceptions of both the nymphs and the *Archodonata* and thus have prevented the publication of what certainly must be one of the most futile articles in all the literature on fossil insects. That the nymphs from the Midco beds are in fact members of the genus *Protereisma* will become obvious from the following account. Since the Moravian specimens are not available to me, I am unable to comment on them except by inference.

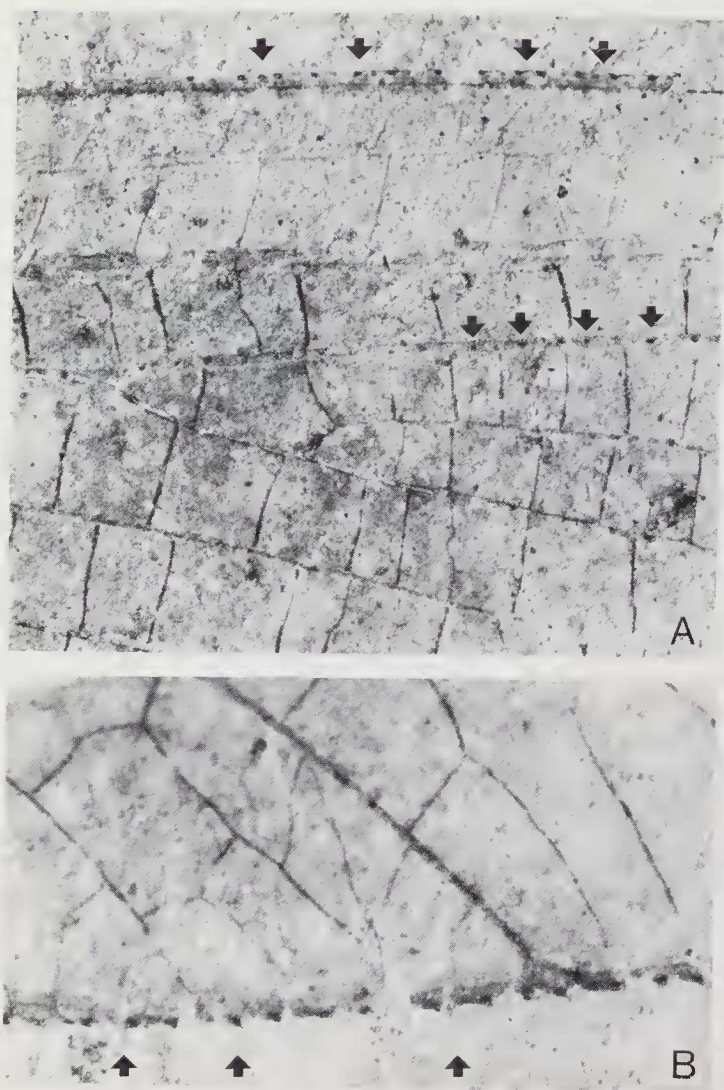


Figure 5. *Protoreisma latum* Sellards. Photographs of neotype, MCZ 3419a, from Permian of Kansas, showing A, anterior part of hind wing, the arrows pointing to setal bases along the front margin of the wing and on certain veins ($\times 24$); B, posterior part of same wing, the arrows pointing to the serrated hind margin ($\times 38$).

Specimens of the mayfly nymphs are by far the most numerous of all the insects in the Midco deposit. Several hundred were collected on my 1940 trip, when Dr. Raasch and I made the first exploration of the deposit, and as many again were collected on subsequent trips. Double that number were simply discarded in the field. Because of their number and the nature of their preservation, it is virtually certain that these fossils are the cuticular remains shed by the nymphs at molting. More than 90% of the specimens consist of isolated wing-pads from the nymphs and most of the remainder represent a single thoracic segment with two wing-pads attached. Only a very few consist of the entire nymph, with all wing-pads and many body structures, these being the specimens that I turned over to Dr. Kukalova in 1969. Since she has given a detailed account of these specimens, I will include here only the salient features, with special reference to the venation of the wing-pads.

The head of the nymphs was slightly narrower than the prothorax, and had well developed, dentate mandibles; the antennae were slender; the prothorax about half as long as the mesothorax, and the meso- and metathorax nearly equal; the legs were subequal, with five tarsal segments; abdominal segments subequal, the cerci and caudal filament well-developed; nine pairs of tracheal gills were present on the abdomen, the anterior ones somewhat larger than the others.

The wing-pads were well developed but were attached to the thorax only along the articular area (of the adult wing), and were independent of each other; the pads projected posteriorly at an oblique angle to the longitudinal axis of the body. The venation of the wing-pads was described by Kukalova, but unfortunately her figure (1969, figure 2) and her interpretation of the homologies of the veins were incorrect. The most conspicuous feature of the venational pattern of the nymphal wings is the difference in the apparent degree of development of the convex and concave veins. In the wing of an adult mayfly (figure 8), the *convex* veins include, in addition to the main veins R1, MA, and CUA, the intercalary veins of the radial sector and of the posterior media; the *concave* veins include, in addition to the main veins RS, MP, and CUP, the intercalary veins of the anterior media and the anterior cubitus. In the Midco nymphs (figure 9) all of the convex veins are very strong and distinct but all of the concave veins are weak and indistinct. Comparison of the nymphal wing with the adult wing of *Protereisma* (figure 8) shows



Figure 6. *Protereisma americanum* (Demoulin), nymph. Photograph of holotype, MCZ 6311, Permian of Oklahoma. Length of body, 16 mm.

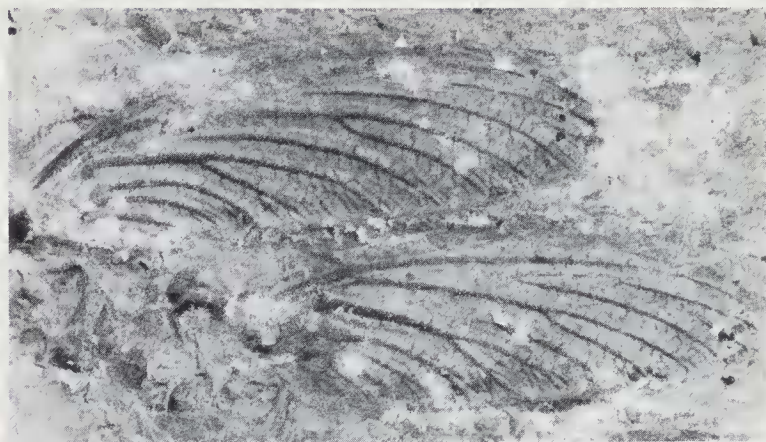


Figure 7. *Protoreisma americana* (Demoulin). Photograph of fore and hind wing-pads of holotype. The dark veins are convex, the weak ones (hardly visible) are concave. Length of fore wing-pad, 5.5 mm.

the precise correspondence of the heavy (convex) veins of the nymphal wing pad with the convex veins of the adult wing, including the intercalary veins of the radial sector and the posterior media. Kukalova, in her interpretation of the nymphal wings, apparently assumed that all of the heavy veins were the main veins and that all of the weak veins were the intercalary veins. As a result, the true MA was included in her radial sector, the true MP was termed MA, CUA was termed MP, and 1A was termed CUP, etc. In figure 9 I include a drawing of the front wing-pad of a nymph (MCZ 8637) with the correct interpretation of the venation. A photograph of the fore and hind wing-pads of the holotype of *americana* is in figure 7.

It is at once obvious from the venation that these nymphs do indeed belong to the genus *Protoreisma*. The presence of the deep fork and triad on CUA eliminates them from the Misthodotidae, for reasons shown below. Demoulin, in removing the nymphs from the Ephemeroptera, was clearly misled by Kukalova's account of their venation but his assignment of them to the order Archodonata was indefensible. The Archodonata had haustellate mouthparts, whereas the nymphs had well developed mandibles. Also, the Archodonata lacked the costal brace, as well as the system of triads and intercalary veins, so well developed in the nymphs.³

³In my opinion the Archodonata are members of the order Palaeodictyoptera.

The family name Kukalovidae Demoulin is consequently a synonym of Protereismatidae and the generic name *Kukalova* is a synonym of *Protereisma*. However, since there are adults of several species of *Protereisma* known in the Midco beds, and since there is no way of correlating the nymphs specifically with the adults, a different specific name is needed for the nymphs from the Midco beds. For this, of course, the name *americana* must be used. I can make no definite comment about the systematic position and nomenclature for the Moravian nymphs described by Kukalova and named by Demoulin. Examination of the original nymphs would be necessary to clear up the uncertainties of the venation. However, on the basis of Kukalova's figure, I think it unlikely that the nymph which Demoulin named *Kukalova moravica* is a protereismatid.

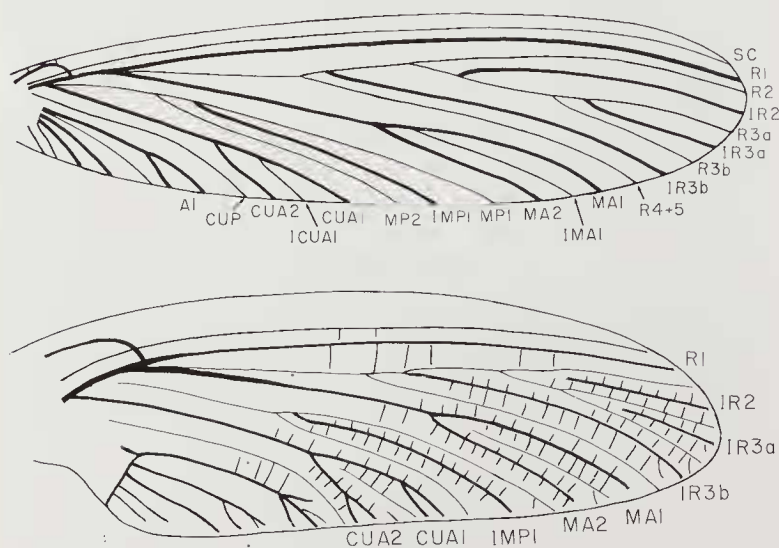


Figure 8. (above) *Protereisma permianum* Sellards. Diagram of venation of fore wing of neotype, MCZ 3405, Permian of Kansas. Convex veins are shown in heavy lines, concave veins in thin lines. Compare with figure 9. Lettering as in figure 2. A1, first anal vein; IR2, IR3, IMA, IMP, and ICUA, intercalary veins.

Figure 9. (below) *Protereisma americanum* (Demoulin). Drawing of fore wing-pad, based mainly on MCZ 8637. Length of wing-pad, 5 mm. Compare with figures 8 and 10. Lettering as in figure 8, but only convex veins labeled.

Protereisma americana (Demoulin)

Figures 6, 7, 9 and 10

Kukulova americana Demoulin, 1970:6

The holotype specimen is numbered 6311ab, Museum of Comparative Zoology; collected by F. M. Carpenter, locality 15-L, Midco insect bed, Noble County, Oklahoma, in 1940 [type designated by Demoulin by reference to plate 29 and figure 1 in Kukulova, 1969]. This specimen, undoubtedly consisting of the cast cuticle of a nymph, shows the general body structure as well as the four wing-pads. Its dimensions are as follows: fore wing-pad, 5.5 mm long, 1.5 mm wide; hind wing, 4.5 mm long, 1.3 mm wide. The body is 16 mm long, exclusive of the terminal appendages and antennae. A detailed description of this nymph is given in Dr. Kukulova's paper and a photograph of the specimen is included here for convenience of reference (figure 6). This is the best and oldest of the mayfly nymphs that have been found in any Palaeozoic deposit. In addition to the type, there are four other specimens (MCZ 8641-8644) showing the gills and other characteristic features; all are about 10 mm long, much smaller than the type, and their wing-pads are very small or absent. As noted above, isolated wing-pads are very numerous in the Midco beds. All have the basic pattern of *P. americana* but of course they may represent more than one species. The smallest (MCZ 8638) of these pads is 2.8 mm long and 1 mm wide (figure 10A); this shows the venational pattern clearly as well as the convexity and concavity of the veins. The largest pad (MCZ 8636) is 7 mm long and 2.2 mm wide; the cross veins and concave veins are more distinct than in the others (figure 10D). Most of the wing-pads are 5.5 mm long and about 1.7 mm wide (figures 10B, 10C).

There are two aspects of these wing-pads, briefly noted above, that are of unusual interest. One is the distinct fluting of the pads, even small ones, resulting from the convexity and concavity of the developing veins. The fluting seems to be much more pronounced in

Figure 10. *Protereisma americanum* (Demoulin). Photographs of wing-pads in several stages of development. A, smallest wing-pad found, 2.8 mm long, 1 mm wide, showing definite convexities and concavities; MCZ 8638, Permian of Oklahoma. Lettering as in figure 9. B, wing-pad 5 mm long, seen under oblique lighting; MCZ 8639. C, same specimen as shown in B but with flat lighting, showing the intensity of the convex veins. D, largest wing-pad found, 7 mm long, the concave veins somewhat more distinct; MCZ 8636, Permian of Oklahoma.



Figure 10

the fossil nymphs than in existing ones. It is possible that the greater amount of fluting, which presumably strengthened the wing-pad, may have been correlated with the limited attachment of the pad to the thorax. In this connection it is pertinent to note that wing-pads of the nymphs of the Palaeodictyoptera and Megasecoptera, which also had the limited attachment to the thorax, show a strong fluting.

A second feature of interest is the marked difference in the fossil nymphs between the convex and concave veins. The convex veins are preserved as dark brown, thick lines, whereas the concave veins are almost without pigment and appear as fine lines. Even the cross veins (see figure 7) are more obvious than the concave veins. If our inference is correct that these wing-pads represent the cast cuticle of the nymphs, then the dark lines seem to have been pigmented thickenings on the cuticle that was cast off in molting. I have no explanation for the difference in appearance of the convex and concave veins. The pattern of difference is the same in both obverse and reverse halves of the fossils. This eliminates the possible inference that the pattern might have been different on the dorsal as opposed to the ventral surface of the wing-pads.

Family Misthodotidae Tillyard

Misthodotidae Tillyard, 1932: 260

Eudoteridae Demoulin, 1954: 561. New synonymy.

The misthodotid adults were of moderate size and generally much smaller than the protereismatids. The wings were broadly oval, usually with maculations, and the hind wings were similar to the fore wings in form and venation, but distinctly broader and with a strongly curved posterior margin. The costal margin was serrate (at least in *Misthodotes*). The costal brace, although distinct, was weaker than in the Protereismatidae. The venation was basically like that of the protereismatids, except that CUA was unbranched and therefore lacked the triad. Cross veins were somewhat less numerous than in the protereismatids. The body structure is not well known. The antennae were like those of the protereismatids and the mandibles were similarly developed. The legs, however, were apparently much shorter and apparently heteronomous, the fore legs being shorter than the others. The tarsi included four segments (at least in *Misthodotes*), the 2nd and 3rd being the shortest. The cerci and median caudal filament were very long.⁴

This family was originally described from the Elmo beds in Kansas. Tschernova (1965) has described adults of two species of *Mis-*

thodotes (zalesskyi and sharovi) from the Permian of Chekarda in the Soviet Union.⁵ These adults appear to be typical of the family except for the tarsal structure, as noted below. Kinzebach (1970) has published an account of a supposed mayfly from the Permian of Germany and has placed it with some question in the family Misthodotidae. Since the wing venation is not preserved, there is no evidence that the specimen belongs to the Ephemeroptera. If it does, the long, slender legs would be more suggestive of the Protereismatidae than the Misthodotidae.

The nymphs of the Misthodotidae are not definitely known. Tschernova (1965) has described a fragment of a nymph from the Chekarda beds and identified it as belonging to *Misthodotes sharovi*. The nymph has nine pairs of gill plates, as in the protereismatid nymphs, but since the entire thoracic region, including the wing pads, is not preserved, there is really no evidence for associating the specimen with *Misthodotes* or even with its family.

There are several adult specimens of Misthodotidae in the MCZ collection from the Midco beds, all belonging to the genus *Misthodotes*. Study of this material and reexamination of the Elmo species have indicated that some revision of the diagnosis of the genus is necessary.

Genus *Misthodotes* Sellards

Dromeus Sellards, 1907: 351 (nec *Dromeus* Reiche) Type species, by monotypy, *D. obtusus* Sellards.

Misthodotes Sellards, 1909: 151. Tillyard, 1932: 261; Carpenter, 1939: 63.

Eudoter Tillyard, 1936: 443. New synonymy.

⁴In one Elmo specimen of *M. obtusus* (MCZ 4388ab) the cerci and the caudal filament, apparently complete, are 20 mm long, or about two and one-half times the length of the abdomen. The full length of the cerci or the caudal filament is unknown in *Protereisma*.

⁵However, Tschernova's account of these fossils is very confusing: the labeling of the veins in the drawings of the wings is different from the terminology used in the descriptions. In her discussion of the venation she states that CUA is either unbranched (i.e., simple) or possesses only a short terminal fork, as is characteristic of the genus *Misthodotes* and its family. But in the figures of both species she has shown CUA as consisting of two long branches, labeled CUA1 and CUA2. The convexities and concavities of the veins are not indicated in her figures, but in the Oklahoma and Elmo specimens of *Misthodotes* the long branch that she has labeled CUA2 is concave and is obviously CUP. The two veins that she has labeled CUP1 and CUP2 are of course anal veins.

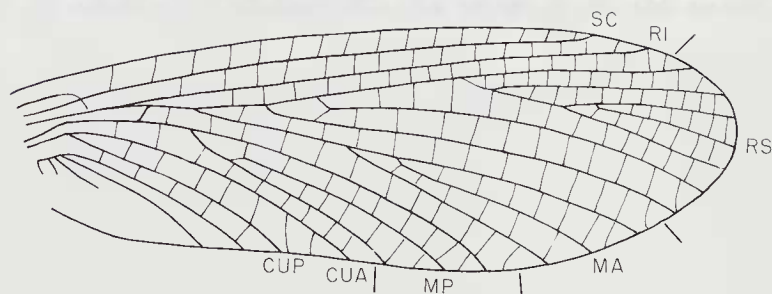
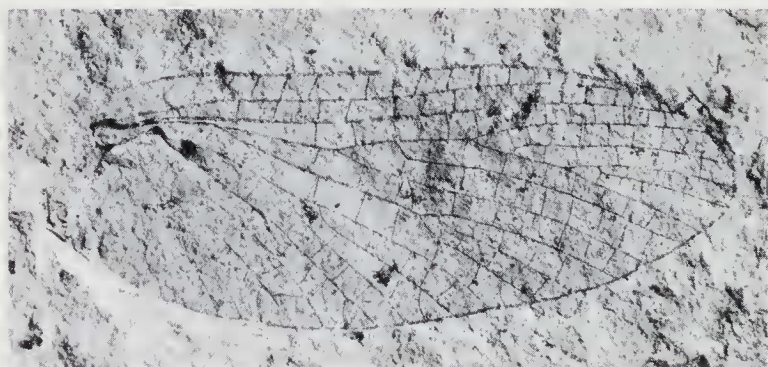


Figure 11 (above). *Misthodotes obtusus*. Sellards. Photograph of hind wing (neotype): YPM 5470, from Permian of Kansas. Length of wing, 10 mm.

Figure 12 (below). *Misthodotes obtusus* Sellards. Drawing of fore wing, based on MCZ 4386ab, from Permian of Kansas. Length of wing, 10 mm. Lettering as in figure 2.

Since the type of *obtusus* was accidentally destroyed in 1927, I subsequently designated (1933) specimen numbered YPM 5470 in the Peabody Museum at Yale University as the neotype of *obtusus*.

The differences between the fore and hind wings of *Misthodotes* and the nature of the cubital-anal area of the wings have not been definitely known. From a survey of all the Elmo specimens in both the Peabody Museum and the MCZ collections, I believe that we can now make a better diagnosis of the genus than has previously been possible and it seems advisable to summarize that before continuing with the account of the Midco specimens.

The best specimen of the fore wing of *obtusus* from Elmo is MCZ 4386, which shows the complete venation, except for the cubital-anal region (figure 12). It should be noted that the costal area near

the wing base does not gradually narrow but ends abruptly. The best specimen of the hind wing is YPM 5470 (figure 11), a drawing of which was given by Tillyard (1934). However, in his figure the costal area is shown as gradually tapering in the region of the costal brace. Although Tillyard stated in his description that the costal vein was obsolescent near the base, on examining the specimen I found that the base of the costa was only covered by a small piece of the rock matrix. On removing that I found that the costal area at the base was in fact like that of the fore wing, not gradually but abruptly narrowed. This is significant because one of the Midco species does have the costal margin gradually narrowed. In the same figure Tillyard included the veins of the cubital-anal area, although I find that there are only vague suggestions of them in the specimen. This area is not clear in any of the Elmo specimens of *obtusus*, either, but it is well preserved in one of the Midco specimens of *Misthodotes ovalis*, mentioned below.

The body structure is not so well known for *Misthodotes* as it is for *Protereisma*. One of the Elmo specimens of *obtusus* in the Peabody Museum (YPM 1100) does show some details. In his description of this specimen Tillyard stated that the tarsi were entirely missing. However, one hind tarsus has now been completely exposed by removal of some of the rock matrix, and its structure

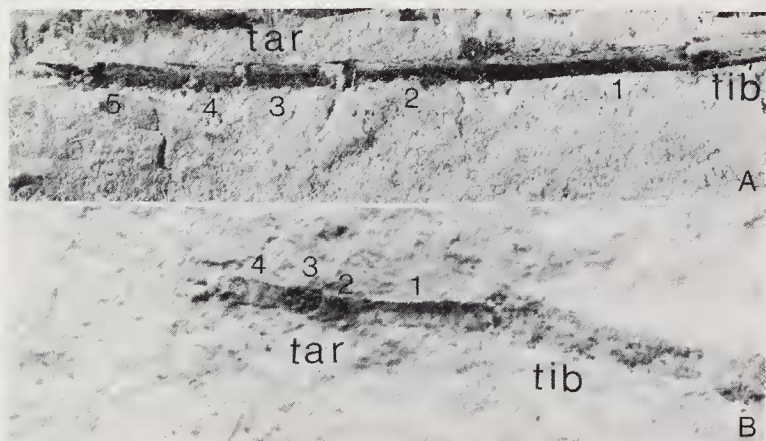


Figure 13. Photographs of tarsi of Protereismatidae and Misthodotidae: A, *Protereisma permianum*, MCZ 3402, Permian of Kansas. Length of tarsus, 8 mm. B, *Misthodotes obtusus*, MCZ 3402, Permian of Kansas. Length of tarsus, 1.5 mm. TIB, tibia; TAR, tarsus.

turns out to be like that which I described in one of the MCZ specimens (Carpenter, 1939): relatively short and consisting of only four segments, the middle two being much shorter than the others (figure 13). This is in marked contrast to the protereismatid tarsi, which were very long and included five segments, the first being the longest and the others subequal.

In this connection it should be noted that Tschernova has described (1965) the tarsal structure of a specimen of a mayfly from the Permian of Chekarda. The species (*sharovi*) was placed in the genus *Misthodotes* and its venation, as noted above, appears to be typical of that of the Misthodotidae. However, the tarsal segmentation is apparently different from that of *M. obtusus*, there being five segments, the fifth being the longest, according to Tschernova's description. Unfortunately, it is not clear from the description whether that segmentation is very distinct or only vaguely preserved. Of course, generic and family definitions are difficult to decide on for the few Permian species of mayflies that are known and it could well be that tarsal segmentation is not significant for the definition of these particular genera or families. However, for the present it seems advisable to consider the assignment of *sharovi* to *Misthodotes* as doubtful.

Of the seven specimens of *Misthodotes* in the Midco collection three belong to the following new species:

***Misthodotes edmundsi*, n.sp.**

Figures 14 and 15

Hind wing: length, 10 mm; maximum width, 3.5 mm. Costal margin straight near mid-wing and curving towards SC well before the midpoint of the costal brace, the costal area gradually tapering towards the base; hind margin smoothly curved, the wing broadest at the level of mid-wing; venation essentially as in *obtusus*; two large, irregular maculations, one at mid-wing, its center about at the fork of R2+3 and R4+5; the other one smaller, just beyond the fork of R2+3. Holotype: No. MCZ 5184ab, collected at locality 15, lower layer, Midco insect bed, Noble Co., Oklahoma, by F. M. Carpenter (1940). This is a perfectly preserved hind wing (figure 14). Paratypes: no. MCZ 5194, a hind wing, complete but not so well preserved as the holotype; length, 10 mm., width, 3.5 mm.; no. MCZ 313ab, a hind wing, complete; length 9 mm.; width, 3 mm.

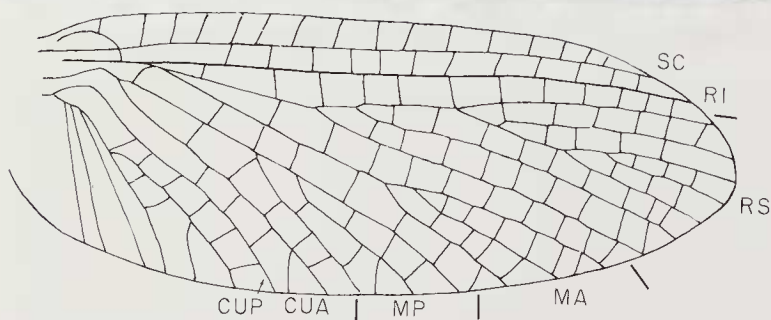


Figure 14 (above). *Misthodotes edmundsi*, n.sp. Photograph of holotype, MCZ 5184 (hind wing). Length of wing, 10 mm. Permian of Oklahoma.

Figure 15 (below). *Misthodotes edmundsi*, n.sp. Drawing of holotype. Lettering as in figure 12. Permian of Oklahoma.

This species is named for Dr. George F. Edmunds, Jr., University of Utah, in recognition of his outstanding contributions to the study of mayflies. The species is close to *obtusus* but differs in the wing shape; in *obtusus* the costal margin is consistently slightly concave, and the costal area remains wide until the very base of the wing; the maximum width of the wing of *obtusus* is nearer the base. Also, the wing of *obtusus* lacks maculations. In addition to wing shape, *edmundsi* differs from *biguttatus* (from Elmo) in having the center maculation much larger and irregular.

Two other specimens from the Midco beds are apparently *Misthodotes ovalis* Tillyard, a species described from Elmo on the basis of a single wing. This is the largest species of *Misthodotes* known;

the wing of the type was 15 mm long and the Midco specimens are fully that size. One of these, a forewing (MCZ 5193) has the cubital-anal area very well preserved and it also shows the large humeral plate at the base of the costal area, as in the holotype specimen of *ovalis*. The two remaining specimens of *Misthodotes* are too incomplete for generic determination.

The Families Eudoteridae and Doteridae

Eudoter delicatulus, described by Tillyard from the Elmo beds (1936), was based on a very poorly preserved specimen. It was placed by him in the family Doteridae Handlirsch (1919), the status of which is discussed below. In 1954 Demoulin proposed the family name Eudoteridae for the genus. He considered it to be close to the Protoreismatidae, from which he thought it differed by its "simplified venation." The type specimen of *delicatulus* (YPM 1014ab), which I have examined on several occasions, consists of part of the body and three folded and badly distorted wings. That the insect is a mayfly is shown by the presence of the median caudal filament between the paired cerci. However, its wing venation, so far as it is preserved, is no more simplified or reduced than that of the Misthodotidae. Indeed, a comparison of Tillyard's drawing of the wing of *delicatulus* (1936, fig. 3) with that of the wing of *Misthodotes* (1932, fig. 20) shows that the *preserved* parts of the wing of *delicatulus* are virtually identical with the corresponding parts of the *Misthodotes* wing. Tshernova (1965), accepting the family Eudoteridae, thought that its cross veins were more poorly developed than in the Misthodotidae. However, in the type of *delicatulus* the cross veins are as abundant and distinct as they are in some specimens of *Misthodotes obtusus*. In his restoration of the wing of *delicatulus* Tillyard represented CUA with a deeply forked triad—but only by broken lines, which he stated in the legend to the figure meant that he was not certain that the triad was present. From my own examination of the specimen under various types of illumination, I am convinced that the veins of the cubital-anal area are simply not preserved, and that there is no indication of the triad on CUA (as Tshernova, 1965, correctly inferred). I am therefore of the opinion that *delicatulus* is a misthodotid and even a member of the genus *Misthodotes*. The species is distinguished by its small size; its wings are only 6 mm long, a little more than half the size of *obtusus*.

The status of the family Doteridae Handlirsch is a more difficult problem. The original specimen of *Doter minor* Sellards (1907) consisted of two folded and twisted wings (both apparently fore wings) and part of the body, including the abdomen (Sellards, 1907, figure 13). When I examined the type in 1926 in Dr. Sellards' laboratory, I was surprised by its poor preservation. As Sellards correctly stated, the median caudal filament was not present and the clear preservation of the two cerci is almost conclusive evidence that the caudal filament was not present in the living insect. Its absence, in even vestigial form, would seem to eliminate the insect from the Ephemeroptera, since it is present in all the specimens of Palaeozoic and Mesozoic mayflies in which the abdomen and cerci are preserved. It is also present, at least in reduced form, in virtually all existing mayflies. The venation of the type specimen of *minor* was so poorly preserved that I would have doubted that the specimen was actually the one described by Sellards, if the abdomen and cerci had not been formed as they were figured by him. The presence of well-developed cerci and the absence of the caudal filament are characteristic of a number of Elmo insects, such as the Asthenohymenidae (Diaphanopteroidea) and Protohymenidae (Megasecoptera). The poorly preserved wings of *minor* did in fact have some resemblance to those of *Asthenohymen* Tillyard, as previously pointed out by Martynov (1930), and in my first account of that genus (1930) I considered *dunbari*, the type of *Asthenohymen*, to be a synonym of *Doter minor*. Since Tillyard did not accept that synonymy and since the type of *Doter minor* had been destroyed by then,⁶ I suggested (1932) that *Doter minor* be regarded as an unrecognized species and that *Asthenohymen dunbari* be accepted as the valid name for the species described by Tillyard. That proposal has subsequently been generally followed, although Demoulin has continued to recognize the family Doteridae as belonging to the Ephemeroptera, regardless of the absence of the median caudal filament. It is highly probable that we may never find a specimen in the Elmo or Midco beds that fits Sellards' description of *minor*. Some 20,000 insects from those two beds have now been examined and none agree with his account of that insect. For this reason I believe that

⁶A few weeks after my return to Cambridge from the University of Texas in 1927, Professor Sellards informed me that during the process of renovating the building in which his laboratory was housed some workmen, thinking that the pieces of the Elmo limestone were fragments of the old walls, threw them out with the general debris.

we should consider *Doter minor* as a species *incerti ordinis* within the Palaeoptera, instead of trying to fit it into the Ephemeroptera.

Order Palaeodictyoptera

The Palaeodictyoptera were apparently already on the wane even by the early Permian. In terms of both species and individuals the members of the order are only sparsely represented in Permian deposits. Only three species of the order have been found in the Elmo beds in Kansas. Two of these, *Calvertiella permiana* Tillyard and *Elmobia piperi* Carpenter, are known only by the holotypes. The third species, *Dunbaria fasciipennis* Tillyard, is represented in the collections of the Museum of Comparative Zoology and the Peabody Museum by ten specimens.⁷ Only one specimen of the order appears to be in our collection from the Midco beds. This is undescribed and is a member of the family Calvertiellidae.

Family Calvertiellidae Martynov

This family includes three species: *Calvertiella permiana*, from the Permian of Kansas, *Moravia convergens* Kukalova (1964), from the Permian of Moravia, and *Carrizoptera arroyo* Kukalova-Peck (1976), from the late Upper Carboniferous of New Mexico. Among the peculiar features of this family is the presence of intercalary veins, which are secondary veins inserted in forks of main veins and which have the opposite topography of the forked veins. They are consistently present in the Protodonata, Odonata, and Ephemeroptera, and occur sporadically in some other orders (e.g., Neuroptera). The presence of intercalary veins in insects that otherwise appeared to be Palaeodictyoptera was first noted in the family Syntonopteridae, which had such veins between the branches of RS, MA, MP, and CUA (Handlirsch, 1911; Carpenter, 1938).⁸ Their occurrence between branches of RS and MP in *Calvertiella* was responsible for Tillyard's placing the genus in the Protodonata. In *Moravia conver-*

⁷Although *Permonera lameerei* Carpenter was originally described as a palaeodictyopteron (1931), it now seems preferable to assign it to the category *incerti ordinis* until more is known about the insect (see Carpenter, 1976).

⁸This has led some students of the Ephemeroptera to conclude that the Syntonopteridae were mayflies, instead of Palaeodictyoptera. This question will probably not be settled until the mouthparts of the syntonopterids are known to be either haustellate as in the Palaeodictyoptera or mandibulate as in the Palaeozoic mayflies.



Figure 16. *Moravia grandis*, n.sp. Photograph of holotype, MCZ 8647a; maximum length of preserved part of wing, 74 mm. Permian of Oklahoma.

gens the intercalary veins were also confined to the branches of RS and MP but were very irregular and formed by alignment of the sides of the two rows of cells bordering the main veins. In *Carrizoptera arroyo* they are so short and irregular as to be hardly recognizable. In the new species, *Moravia grandis*, described below, the radial sector is not preserved, but the intercalary veins are not present between the branches of MA, MP, or CUA, the spaces between the veins being filled with a reticulate archdictyon. The nature of the intercalary veins in the Calvertiellidae, therefore, would seem to suggest that these veins developed in that family quite independently of their occurrence in other orders or families. They appear to have arisen by the alignment of the sides of the cells forming the archdictyon between the main veins. The development of such intercalary veins, in association with the increased fluting along the veins, may have provided more support for the wing membrane than the original archdictyon. In any case, I believe that the presence or absence of the intercalary veins should not be given very much weight in considering evolutionary relationships.

Genus *Moravia* Kukalova

Moravia Kukalova, 1964: 162; Kukalova-Peck & Peck, 1976:83.

This genus is characterized by the presence of an arched cuticular strut, formed by the alignment of the basal parts of R1 and CUA, connected by a strong cross vein. It has previously been known only by the type-species, *convergens*, from the Lower Permian of Obora, Czechoslovakia.

***Moravia grandis*, n.sp.**

Figures 16 and 17A

Hind wing: maximum length of preserved portion, 72 mm; maximum width, 48 mm; estimated length of complete wing, based on *M. convergens*, 90 mm. The basic pattern of the main veins, so far as preserved, is very similar to that of *convergens* (figure 17B). CUA, CUP, and 1A are not so strongly curved as in *convergens* and the spaces between the main veins are filled with several rows of cells forming the archdictyon in the distal portion or by fine, irregular crossveins in the basal portion. This is a very distinct species and may eventually require a separate genus. However, until the distal part of the wing is known, it seems preferable to assign the species to the genus *Moravia*.

Holotype: no. MCZ 8647ab, collected at locality 1, lower layer, in the Midco beds, Noble County, Oklahoma, by F. M. Carpenter in 1940. This consists of the basal two-thirds or three-fourths of a hind wing, with all details very well preserved. The distal part of the wing appears to have been torn away before preservation. This species is by far the largest known in the family Calvertiellidae, being apparently more than twice the size of *convergens* and more than three times the size of *permiana* or *arroyo*.

Comparison of the Species of Palaeoptera in
the Elmo and Midco Beds

In my introduction to Part 1 of this series of papers (1947) I pointed out that the Elmo beds in Kansas and the Midco beds in Oklahoma originated as deposits formed by lakes about 140 miles apart. Both deposits are part of the Wellington Formation of the Leonardian Stage of the Permian and, in geological terms, were

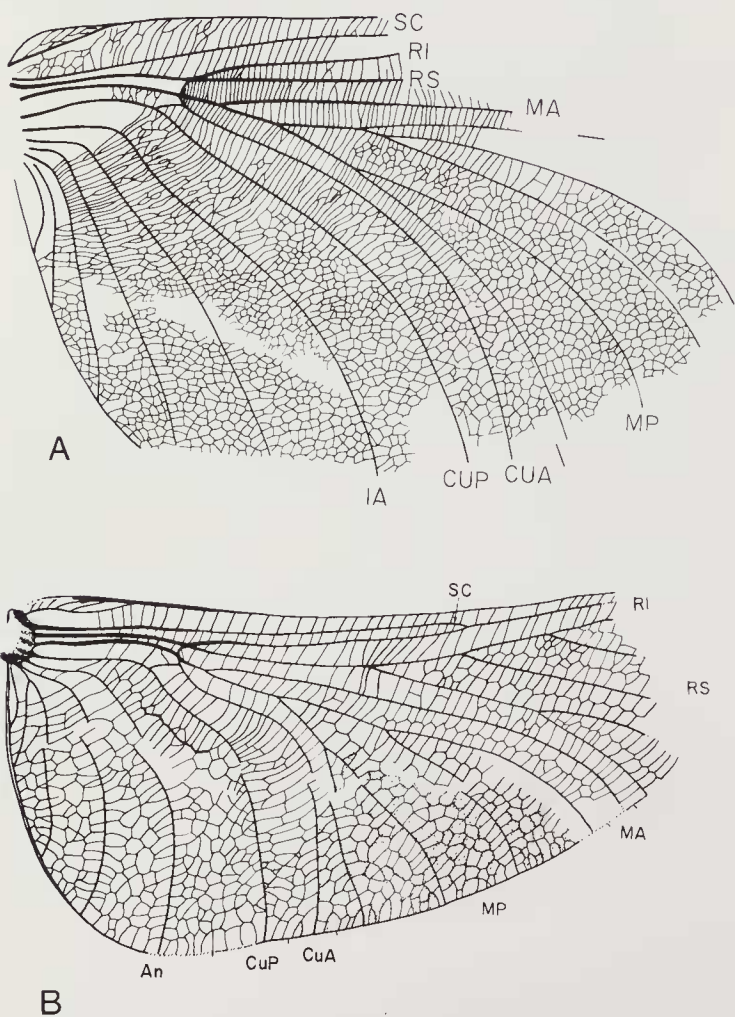


Figure 17A. *Moravia grandis*, n.sp. Drawing of holotype. Lettering as in figure 12. Permian of Oklahoma.

Figure 17B. *Moravia convergens* Kukulova. Drawing of paratype (hind wing). Lower Permian of Moravia. [From Kukulova, 1964].

Table 1 Comparison of Paleopterous Species from Elmo and Midco Beds

ORDERS	NUMBERS OF SPECIES		
	<i>Elmo</i>	<i>Midco</i>	<i>Elmo & Midco</i>
Palaeodictyoptera	3	1	0
Megasecoptera	5	5	1
Diaphanopteroidea	7	14	3
Protodonata	5	3	1
Odonata	4	5	2
Ephemeroptera	8	5	1
	32	33	8

apparently contemporaneous. However, there appear to have been differences in the environments of the lakes (Raasch, 1946). The one in Kansas contained fresh water, derived from an earlier swamp, with plants growing close to the water's edge and with some insect nymphs living in the water. The Midco lake was essentially a playa, containing algae and Conchostraca; plants did not grow near it and insect nymphs did not live in it.⁹

Now that the study of the Palaeoptera in the Midco beds has been completed, it is of some interest to compare the numbers of species represented in each deposit and common to both deposits. These figures are given in the accompanying table (Table 1). The total number of species in each of the beds is very close, and the number of species in each order corresponds closely except for the Diaphanopteroidea, of which there are twice as many in the Midco beds as at Elmo. It appears that, on the average, about one-quarter of the Midco species collected also occur at Elmo.

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⁹The fossil mayfly nymphs discussed above were apparently the cuticular remains shed by the nymphs at moulting and carried down streams to the lake.

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